Understanding agriculture within the frameworks of cumulative cultural evolution, gene-culture coevolution and cultural niche construction

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Abstract

Since its emergence around 12,000 years ago, agriculture has transformed our species, other species, and the planet on which we all live. Here we argue that the emergence and impact of agriculture can be understood within new theoretical frameworks that are taking hold within the evolutionary human sciences. First, the improvement and diversification of agricultural knowledge, practices and technology is a case of cumulative cultural evolution, with successive modifications accumulated over multiple generations to exceed what any single person could create alone. We discuss how the factors that permit, facilitate and hinder cumulative cultural evolution might apply to agriculture. Second, agriculture is a prime example of gene-culture coevolution, where culturally transmitted agricultural practices generate novel selection pressures for genetic evolution. While this point has traditionally been made for the human genome, we expand the concept to include genetic changes in domesticated plants and animals, both via traditional breeding and molecular breeding. Third, agriculture is a powerful niche-constructing activity, having extensively transformed the abiotic, biotic and social environments. We focus on the latter, and examine how agricultural knowledge and practice shapes, and is shaped by, social norms and attitudes. Throughout, we discuss recent biotechnology and associated molecular breeding techniques, and present several case studies, including golden rice and stress resistance. Overall, we propose new insights into the coevolution of human culture and plant genes, and the unprecedented contribution of agricultural activities to the construction of unique agriculture-driven anthropogenic biomes.

Keywords: agriculture, cultural evolution, gene-culture coevolution, niche construction, GM plants

Introduction

Although once united under the single term “natural philosophy”, for over a century now, scholars within the biological sciences striving to understand and manipulate the natural world have seldom interacted with scholars studying culture and society. This situation is problematic for many reasons, not least the social and cultural consequences of increasingly powerful biotechnology. However, recent developments at the intersection of the natural and social sciences – specifically, theories of cultural evolution, niche construction and gene-culture coevolution – have begun to bridge the gap between the study of biology and culture. In this paper we explore how these new interdisciplinary approaches might contribute to the study of agriculture, which is a topic that straddles the natural-social science divide.

The transition from hunting-gathering to agriculture, observed in most human societies, is a key event in human history that has transformed human societies beyond recognition. For much of its evolutionary history our species practised hunting and gathering, as a few isolated societies still do today (Panter-Brick, Layton and Rowley-Conwy 2001). Beginning around 12,000 years ago, some human populations began domesticating plant and animal species (Fuller et al. 2014; Larson et al. 2014). The adoption of agriculture triggered the establishment of small permanent settlements and then densely-populated cities, kingdoms and states. It saw the creation of new political institutions and forms of social organization and stimulated an upsurge in scientific and technological innovation. It also brought many problems, such as the spread of new diseases and increased social inequality. Agricultural knowledge and technologies have continued to advance at an increasing pace particularly in the last century. The discovery of the rules of genetics by Mendel (Mendel 1866) and their rediscovery around 1900 (Corcos and Monaghan 1990), resulted in the application of plant breeding technologies from the 1930s onwards (Carlson 2004; Koornneef and Stam 2001; Heslop-Harrison and Scwarzacher 2012). The “green revolution” in several developing countries during 1950–1970, which encompassed the use of new high-yield crops, together with fertilizers and pesticides, was an important landmark in agricultural plant breeding, yet still based on traditional Mendelian breeding methods (Farmer 1986). The era of molecular breeding, including marker-assisted selection (MAS), from 1983 onwards (Smith and Simpson 1986, Ben-Ari 2012) was followed by widespread genetic engineering/modification of crop plants (Gasser and Fraley 1989), and more recently by genome editing technologies (Bortesi and Fischer 2015; Sander and Joung 2014). Molecular breeding has transformed agricultural practices worldwide, yet often faces strong public and political opposition.

Despite the importance of agriculture to our species’ history, and the rapid recent advances in molecular breeding technologies, there remain disagreements over which theoretical framework offers the best way to understand the origin, spread and ongoing transformation of agriculture. Several recent debates and exchanges have revealed a tension between, on the one hand, interpretive, humanities-oriented frameworks which focus on culture and agency on the part of agriculturalists and the socio-political contexts within which agriculture is practised, and, on the other hand, neo-Darwinian approaches that use tools such as optimal foraging theory derived from behavioural ecology to understand agricultural decisions, assuming that human decision-making has genetically evolved to maximise inclusive genetic fitness (for examples of this debate see Cochrane and Gardner 2011; Gremillion, Barton and Piperno 2014). The former approaches are laudable in their attempt to situate agriculture within the rich socio-cultural contexts that they demand, yet often lack rigorous scientific methods, and sometimes suffer from the general malaise within the humanities of being politically motivated, agenda-driven, and disconnected from the natural and behavioural sciences (Barkow 2005; D'Andrade 2000; Slingerland and Collard 2011). The latter approaches are often limited in their theoretical assumptions, and, we would argue, do not fully incorporate the role of culture as more than a proximate mechanism (Laland et al. 2011; Mesoudi et al. 2013).

Here we follow others (O'Brien and Laland 2012; Rowley-Conwy and Layton 2011; Zeder 2015) in arguing that the study of agriculture can benefit from being situated within a set of new evolutionary approaches to human behaviour – cultural evolution, gene-culture coevolution and cultural niche construction – that attempt to incorporate cultural change and individual agency within a rigorous, scientific and multidisciplinary evolutionary framework. We highlight several ways in which the study of agriculture can benefit from these frameworks. We also highlight ways in which a consideration of agriculture yields new insights into cultural evolution, gene-culture coevolution and niche construction. Specifically, we argue that (see also Figure 1):

- changes in agricultural knowledge and practices are a prime example of cumulative cultural evolution (CCE), where beneficial ideas and inventions are selectively preserved and accumulate in number and effectiveness over successive generations of people. We apply the large body of modelling and experimental insights already obtained for CCE generally, and apply them to agriculture. This illuminates the recent rapid advance in agricultural knowledge in the last two centuries, and also highlights the role of intentional vs non-intentional modification.

- agriculture is a prime example of gene-culture coevolution (GCC), where culturally-transmitted practices affect a species' genetic evolution, and vice versa. However, this is not just (as frequently argued previously) the case of culturally-transmitted agricultural practices changing human genes, but also changing non-human genes contained within domesticated and genetically modified organisms.

- agriculture is associated with extensive cultural niche construction (CNC), where agricultural practices transform the environment and those environmental changes alter the selection pressures on agricultural CCE. We argue that agriculture can modify (i) the abiotic environment (e.g. water, salinity, soil composition), (ii) the biotic environment (e.g. domesticated species, pests including insects, fungi and weeds), and (iii) the social environment (e.g. social norms, regulation, markets), and focus in particular on the latter.

The following sections take each of these points and expand them in the context of selected examples of plant breeding via new molecular tools. We apply these insights to two case studies, first golden rice, then stress tolerance. We end by highlighting outstanding questions that arise from our attempt to place agriculture within these frameworks.

[insert figure 1 here]

Agriculture as cumulative cultural evolution

For most of the 20th century, the study of cultural change remained largely separate from the biological sciences. From the 1970s, scholars began developing a formal theory of *cultural evolution*, in which cultural change is viewed as an evolutionary process that shares key characteristics with, but differs in important ways from, genetic evolution (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1973, 1981; see Mesoudi 2011a, 2017 for reviews). This approach incorporates cultural change and variation into a theoretical framework that is consistent with the evolutionary sciences. Central to this approach is the idea that cultural change constitutes an evolutionary process in its own right: it is a system of inherited variation that changes over time, just as Darwin defined evolution in *The Origin of Species* (Darwin 1859). 'Culture' is defined here as learned information that passes from individual to individual via social learning processes such as imitation, teaching or spoken or written language. Social learning therefore provides the inheritance system in cultural evolution, paralleling genetic inheritance in genetic evolution.

Recognising this parallel, we can borrow and adapt tools, concepts and methods from the biological sciences to study cultural change (Mesoudi, Whiten and Laland 2006). These include mathematical models (Boyd and Richerson 1985; Cavalli-Sforza and Feldman 1981), phylogenetic analyses (Gray and Watts 2017), lab experiments, archaeological data and field research (Mesoudi 2011a). Importantly, this research does not unthinkingly import genetic models of change and apply them to cultural change without considering the unique aspects of the latter. For example, we can incorporate multiple pathways of inheritance: not just from parents to offspring like genetic evolution, but also transmission from non-parents and between peers (Cavalli-Sforza and Feldman 1981). Psychological processes such as conformity work to favour common behaviours, while prestige bias spreads behaviours associated with high status individuals (Boyd and Richerson 1985). There may be Lamarckian-like transformation such that novel cultural variants are not blind with respect to function (Boyd and Richerson 1985); they may be intentionally created by individuals to solve specific problems. This allows agentic decision-making forces to be incorporated into an evolutionary framework (Mesoudi 2008).

One interesting property of human cultural evolution is that it can be *cumulative* (Tennie, Call and Tomasello 2009). Other species exhibit social learning, and this is sometimes powerful enough to generate between-group behavioural traditions. For example, chimpanzee communities across Africa exhibit group-specific tool use profiles (Whiten 2017). Yet only humans appear able to accumulate and recombine behavioural modifications over time via social learning, generating complex cultural traits that could not have been invented by a single individual alone (Dean et al. 2014; Tennie et al. 2009).

Agriculture is a prime example of cumulative cultural evolution. Other species practice agriculture in a sense, most famously leaf-cutter ants of the genera *Acromyrmex* and *Atta* which cultivate a type of fungus (Schultz and Brady 2008). However, the adaptations responsible for this are genetic, not cultural. Human agriculture is the result of repeated behavioural innovations that spread, accumulate and recombine via social learning through and beyond communities. This allows for great flexibility, often involving the simultaneous use of multiple domesticated species, and more rapid change over time, on the order of thousands, hundreds or tens of years rather than millions as in the case of ant-fungus genetic evolution (Schultz and Brady 2008). In humans, agricultural knowledge, practices and technologies are culturally evolving traits which often show a cumulative increase in scope and complexity over time (Figure 2). Typically, these traits are sequentially linked, with prior inventions necessary for the emergence of subsequent ones. Key innovations include irrigation by controlling water flow via canals and other waterways, the invention of different types of plough, the conversion of gaseous nitrogen to inorganic nitrogen fertilizers to enhance crop yields, the industrial mechanization of a variety of agricultural processes, and the discovery of the principles of genetics that allowed classical plant breeding. Recent CCE has resulted in new agricultural and computerized technologies, e.g. drip irrigation (Camp 1998) and precision agriculture (Mulla 2013), and the application of novel molecular tools for breeding of crops and farm animals, such as the use of in vitro procedures for plant propagation (Loberant and Altman 2010), fertility control and genetic modifications in farm animals (Hasler 2003; Xu et al. 2006) and molecular markers for selection (Smith and Simpson 1986, Ben-Ari 2012), genetically-modified (GM) plants (Gasser and Fraley 1989), and genome editing of crops (Bortesi and Fischer 2015; Sander and Joung 2014). As expected for a historically-contingent, culturally evolving process, these various innovations occurred in stops and starts, showed different trajectories in different societies and were sometimes lost, reintroduced or recombined (Fuller et al., 2014). Agriculture therefore fits several ‘extended criteria’ of CCE specified by Mesoudi and Thornton (2018): not just repeated improvement as a result of individual and social learning, but also sequential dependence of innovations, branching lineages and recombination across lineages.

[insert figure 2 here]

Viewing agriculture as CCE allows us to draw on the large body of formal models and experiments that have explored the factors that allow, facilitate and constrain CCE and apply these insights to agriculture. CCE is thought to depend on high fidelity social learning, which is required to faithfully preserve beneficial innovations across generations and over time (Lewis and Laland 2012). This social learning also needs to be selective, either selectively preserving successful practices, or selectively learning from successful individuals (Laland 2004; Mesoudi 2011b). In the context of small scale agriculture, this may involve the observation of, or teaching by, expert plant and animal breeders. Since the emergence of formal systems of science, one-to-one transmission has been replaced by the transmission of knowledge in publications such as journals, books and patents, which would greatly increase the fidelity of social learning.

Equally important to mechanisms of social learning are aspects of demography. In order to support continued CCE, populations must be large enough to sustain the repeated transmission of knowledge (Henrich 2004; Powell, Shennan and Thomas 2009), and they should also ideally be partially connected, e.g. via migration, such that different innovations can emerge in different groups and then become recombined, rather than the entire population fixating too soon on a single suboptimal solution (Derex and Boyd 2016). The recombination of beneficial traits can generate exponential increases in knowledge, as seen in the patent record (Youn et al. 2015).

Finally, the type of innovation can affect the dynamics of CCE. Miu et al. (2018) found, in a computer programming tournament, two classes of innovations: small, incremental ‘tweaks’ that were common but unlikely to lead to major increases in performance, and rarer ‘leaps’ that made bigger changes to existing knowledge, were more likely to fail, but had a small chance of a major improvement. These rare innovative leaps may play a disproportionate role in CCE (Kolodny, Creanza, and Feldman 2015). The novel innovations listed in Figure 2 can be seen as examples of these.

An interesting question is whether innovation is intentional or not. In genetic evolution, there is no foresight. Genetic mutations arise randomly with respect to their adaptive effects; beneficial mutations are no more likely to arise when they are needed than when they are not. In cultural evolution, however, innovation may be intentionally directed in ways that make adaptive variants more likely to occur. This foresight can never be perfect (people are not omniscient: Mesoudi 2008), but this intentionality may speed up CCE compared to if modifications were random, as suggested by models of ‘guided variation’ (Boyd and Richerson 1985) and ‘iterated learning’ (Griffiths, Kalish and Lewandowsky 2008). On the other hand, major innovative leaps in CCE often arise by accident, suggesting that randomness can be useful; classic cases include the discovery of Penicillin and x-rays (Simonton 1995). Of course, real cases of innovation may involve both chance and intention, as represented by the phrase ‘chance favours the prepared mind’; Alexander Fleming would not have realised the significance of his chance discovery if he had not been prepared to do so. The issue of intentionality in the emergence of agriculture has been debated extensively (Abbo, Lev-Yadun and Gopher 2014; Fuller et al. 2012; Kluyver et al. 2017), often in oppositional terms with some arguing for the role of intentionality and others arguing against. Cultural evolution models, such as those of guided variation, permit the inclusion of both intentional and non-intentional factors, to compare their combined effects on the speed and form of agricultural CCE. Recent GM technology represents however the ultimate in intentional modification, with agricultural CCE no longer dependent on random genetic mutation and recombination to create superior breeds.

Agriculture as a driver of gene-culture coevolution

Gene-culture coevolution incorporates CCE, but focuses on those cases where cultural inheritance causes changes in gene frequencies, which feeds back on cultural evolution, forming a coevolutionary dynamic (Feldman and Laland 1996; Laland, Odling-Smee and Myles 2010). Several classic cases of human gene-culture coevolution involve agriculture, given the growing evidence that agricultural practices have left indelible signatures on the human genome over the last 12,000 years (Laland et al. 2010; Richerson, Boyd and Henrich 2010). O'Brien and Laland (2012) discuss two classic cases: first, the spread of lactose tolerance alleles from around 7500 years ago in central European populations as a consequence of the cultural practice of dairy farming (Gerbault et al. 2011; Itan, Powell, Beaumont, Burger and Thomas 2009); and second, the spread of sickle-cell alleles in West African populations that confer resistance against malaria, which increased in prevalence following the clearing of forests for yam cultivation, which created pools of standing water within which mosquitoes breed (Wiesenfeld 1967). In both cases, there is clear archaeological, anthropological and genetic evidence that cultural practices came first, followed by genetic responses that continue to affect behavioural variation across contemporary human populations.

What is less often recognised in discussions of gene-culture coevolution is that agriculture also causes genetic change in non-human species. Many definitions of agriculture require there to be human-induced genetic change in the domesticated plant or animal (Rowley-Conwy and Layton 2011). This non-human genetic change may be the result of intentional or unintentional artificial selection for traits that increase yields, or side-effects of such selection. The entire package of genetic changes in a domesticated species is sometimes called the “domestication syndrome” (Larson et al. 2014). There is extensive evidence, particularly since the advent of gene sequencing, for sustained genetic changes in domesticated species of both plants and animals (Zeder 2015). In plants the domestication syndrome may include larger seeds, synchronous germination or fruit ripening that makes sowing or harvesting easier, and reduction in chemical defences (Fuller et al. 2014). In animals, the syndrome includes increased docility, changes in body shape and size, and altered reproduction patterns (Larson and Fuller 2014). In some cases, non-human genetic change coincides with human genetic change, as in the case of lactose tolerance genes in humans and corresponding changes in cattle genes (Beja-Pereira et al. 2003). Genetic modification by conventional and molecular intentional breeding represents further genetic change as a result of agricultural practices, and is covered in later sections in more detail.

Agriculture as niche construction

As O'Brien and Laland (2012) have argued, agriculture is also a prime example of cultural niche construction. Niche construction is the general biological principle that organisms do not just passively adapt to their environments. Often they actively construct their environments, with those environmental modifications in turn affecting their own and other species' evolution (Odling Smee, Laland and Feldman 2003). These modified environments may be inherited via what is termed *ecological inheritance*. Cases of non-cultural niche construction occur in numerous species; examples include earthworms' burrowing and mixing activities which alter soil nutrient content, and beaver dam-building which creates standing water. These activities have evolutionary consequences: for example, earthworms have retained their freshwater kidneys rather than adapt to the terrestrial environment, because the mixed soil that they create allows easier absorption of water (Turner 2000).

Cultural niche construction occurs when the behaviours that modify environments are at least partly socially learned, and the consequences potentially affect subsequent cultural evolutionary dynamics (as well as, potentially, genetic evolutionary dynamics; this would be a case of GCC) (Kendal, Tehrani and Odling-Smee 2011; Laland, Odling Smee and Feldman 2000). The ‘environment’ here can be physical or abiotic (e.g. soil composition or climatic conditions, both of which strongly affect plant development), biotic (composed of other species; in the case of domesticated plants this would include phytopathogenic fungi, bacteria and insects) and social (composed of other individuals of the same species, e.g., competition between neighbouring plants at the root level).

Despite romantic notions of the “noble savage” living passively in an unaltered environment, hunter gatherers frequently engage in cultural niche construction by modifying their environments through cultural practices such as controlled burning of vegetation (Rowley-Conwy and Layton 2011; Smith 2011; Boivin et al. 2016). Large-scale agriculture brought about cultural niche construction orders of magnitude more extensive (O’Brien and Laland 2012; Rowley-Conwy and Layton 2011). Agriculture caused huge changes to physical environments, including the clearing of forests, the irrigation of previously arid environments, the dispersal of domesticated plants and animals, and the introduction of new parasites and pests. Agriculture also brought about huge changes to human social environments, including increased population density and new forms of social organisation (e.g. new forms of hierarchies). Finally, the accumulation of agricultural practices and knowledge shaped environments in which further accumulation of agricultural practices was made more likely; this is the CCE noted above. In fact, large-scale agriculture, which produces the majority of the food consumed worldwide (e.g. rice, corn, wheat, canola, soybean) is generally a monoculture (i.e. a single type of plant species that is cultivated in large land areas as crop for human consumption), unlike home gardens, natural savannahs, pastures and forests which contain many species. Agriculture therefore results in modified niches compared with the natural vegetation, with clear effects on ecosystems (Matson 1997).

A consideration of how agricultural practices shape, and are shaped by, social environments allows us to consider the mutual dynamics between agriculture and the social norms, regulations and markets that often determine whether a particular technology or practice spreads or not. A good example of this is the acceptance and rejection of GM foods, which is covered in the next section.

Case studies: Biotechnology

Most previous discussion of GCC in the context of agriculture concerns deep human history and prehistory, such as lactose tolerance and dairy farming (O'Brien and Laland 2012). In our case studies we instead focus on recent biotechnology and molecular breeding, to illustrate the points raised above, and demonstrate the relevance of these theoretical frameworks to contemporary issues. Moreover, studying recent scientific discoveries and technologies offer richer data for testing theories of cultural change compared to the ancient events of early domestication, which can only be studied indirectly via historical or archaeological methods.

Following the Neolithic agricultural revolution and initial crop domestication, and all subsequent agricultural improvements including traditional breeding methods based on Mendelian genetics, a new agricultural phase occurred in the middle of the 20th century: the era of molecular breeding, genetic engineering and in vitro biology (Fig. 2). While some scholars refer to these as ‘revolutions’ (or at the extreme, a single ‘agricultural revolution’), they are clearly all a process of CCE, with each major advance dependent on previous advances. Molecular breeding and genetic engineering could not have been invented without existing knowledge of Mendelian genetics. Yet, there are differences. The Neolithic agricultural period, i.e. plant and animal domestication, as well as other technological improvements in agriculture and biology (e.g. the use of irrigation and fertilizers) are more protracted and evolved sequentially over a period of hundreds or thousands of years (Fig. 2). In contrast, the time span of adopting and applying molecular plant breeding technologies and in vitro biology has been much shorter. Such technologies emerged far more rapidly, and became a working reality only within the last few decades. The molecular structure of DNA was first published in 1953 (Watson and Crick 1953), and the first genetically modified (GM) or transgenic plant (i.e., produced via incorporation of recombinant DNA), tobacco, was first created in the laboratory in 1982 (De Framond, Barton and Chilton 1983; Gasser and Fraley 1989; Zambryski et al. 1983; Tepfer 1984). Farmers began to plant GM crops in 1996, and in 2017, the 21st year of commercialization of biotech crops, 189.8 million hectares of biotech crops were planted by up to 17 million farmers in 24 countries. From the initial planting of 1.7 million hectares in 1996 when the first biotech crop was commercialized, the 189.8 million hectares planted in 2017 indicates ~112-fold increase, which makes GM crops the fastest adopted crop technology in recent times(Altman and Hasegawa 2012; Farre et al. 2010; ISAAA 2017; Moshelion and Altman 2015). Molecular genetics, including genetic engineering of crops and the use of molecular marker-assisted selection, as well as novel gene editing technologies like the CRISPR/Cas9 system and synthetic biology (Bortesi and Fischer 2015; Baltes and Voytas 2015; Zong et al. 2017) and other in vitro procedures such as in vitro propagation (micropropagation) (Loberant and Altman 2010; Khayat 2012), are currently modifying the breeding opportunities of domesticated and cultivated plants globally (Altman and Hasegawa 2012; Moshelion and Altman 2015; Farre et al. 2010, Potrykus and Ammann 2010). This is also true for in vitro and molecular genetic procedures in farm animals and humans, e.g. in-vitro fertilization (Bavister 2002).

The molecular breeding technology described above is clearly a case of CCE, building on what went before (e.g. Mendelian genetics) and far exceeding what any single individual could achieve alone. The increasingly rapid (i.e. exponential) accumulation of knowledge is a well-known characteristic of CCE (Enquist et al. 2008). There are many potential explanations for this exponential increase, including the recombination of an increasing number of traits (Enquist, Ghirlanda, and Eriksson 2011; Youn et al. 2015) or the enhancement of innovation and discovery as a result of CCE products such as scientific instruments (Enquist et al. 2008; Mesoudi 2011b). Molecular breeding is also a case of GCC, where the genes of other species are directly and intentionally modified using culturally evolving scientific techniques. These genetic modifications in turn demand new and more powerful scientific techniques and knowledge. Finally, molecular breeding involves extensive CNC, in terms of major changes to the abiotic, biotic and social environments, as explored in our specific case studies below.

Case study 1: Golden rice

Rice, originally domesticated in East Asia around 8-9kya, is a major staple food for billions of people worldwide, supplying the majority of energy and carbohydrate requirements in addition to other nutritional factors (Wing, Purugganan and Zhang 2018). Historically, rice is thought to have played a role in human GCC by driving the selection of alcohol dehydrogenase alleles in rice-farming populations in which rice was used in fermentation of food and beverages (Peng et al. 2010). In addition to this long history of traditional breeding, rice has more recently been subject to some of the first molecular breeding.

Rice is generally consumed in its “polished” milled form by removing its outer layers. As a result, the edible part of rice grains consists of the endosperm that contains starch granules and protein bodies. However, this part lacks several essential nutrients that are more abundant in the outer layers of the grain, such as the carotenoid pro-vitamin A (β-carotene), which is converted in the body to vitamin A. Thus, reliance on polished rice as a primary staple food, which is an example of culturally evolving culinary traditions, results in vitamin A deficiency, a serious public health problem which is the primary cause of blindness and other diseases in new-borns in many developing countries (Srikantia 1975).

Conventional breeding of rice to increase vitamin A content is impractical due to the lack of appropriate rice cultivars that produce pro-vitamin A in the grain. Research into the β-carotene biosynthetic pathway resulted in the ability to defeat vitamin A deficiency by genetically transforming commercial rice varieties using two daffodil genes and one bacterial gene, resulting in vitamin A-rich rice (Burkhardt et al. 1997). This genetically engineered, polished, fortified “golden rice” can supply sufficient pro-vitamin A for the body to convert into vitamin A, saving the eyesight and lives of millions of vitamin A-deficient children who are dependent on rice in their basic diet (Potrykus 2001). Subsequent molecular breeding is leading to “green super rice”, a form of rice that has a lower ecological footprint (Wing et al. 2018).

The continual modification and accumulation of GM rice breeds, from traditional rice to golden rice to green super rice, represents a case of CCE, where we see continual improvement in multiple criteria of yield, nutritional quality, fit to local agricultural practices and ecological sustainability. The genetic changes in rice brought about with domestication and selection have been succeeded by traditional breeding and recently by direct, intentional genetic modification, representing a case of GCC between human agricultural scientific practices and rice genomes (as well as human genes, in the aforementioned case of alcohol dehydrogenase).

Rice has also been responsible for extensive CNC. This involves not only the modification of abiotic and biotic environments, but also social environments. One key feedback between agricultural practices and social environments has been oppositional. Like many other GM crops, the adoption of golden rice, despite its health benefits, has been delayed considerably due to legislation, socio-economic issues, and public concerns. Compared to non-GM rice varieties, the adoption and deployment of golden rice has suffered from a delay of more than 14 years. The first scientific procedure was published in 1997. Under regular processes golden rice could have reached farmers' fields in Asia by 2002, but in fact was not approved officially for human consumption, except for planting by selected farmers, until 2013-2014 (Potrykus 2010). The cause of this delay was the demanding GM-regulation process. While regulation is needed to establish public safety, many hurdles existed not because of scientific problems or safety regulation, but rather due to the negative political climate surrounding GM-technology and the activities of anti-GM activists, the lengthy Intellectual Property (IP) rights approval, the lack of financial support from the public domain, and GM-regulation procedures that required several technological solutions (Potrykus 2010). These delays created a situation where no public institution could deliver GM products because of the high expenses of large-scale production, which resulted in a de facto monopoly of a few potent commercial industries that supplied high-priced seeds to farmers. Since then, GR2E Golden Rice, a provitamin-A biofortified rice variety, received its third positive food safety evaluation by the United States Food and Drug Administration (US FDA) on May 2018, following earlier approvals by Food Standards Australia New Zealand (FSANZ) and Health Canada, all based on the principles of the World Health Organization (WHO), the Food and Agriculture Organization (FAO) of the United Nations, and other international agencies (IRRA 2018).

This negative feedback from the social environment in the form of oppositional social norms and increased regulation has prevented the timely adoption of an available solution to vitamin A deficiency, and similar situations exist for other GM crops. GM crops could help solve, together with other technologies, many of the world's most challenging food problems, including hunger, malnutrition, disease and poverty. However, this potential cannot be realized if the major barriers to adoption - which are largely socio-cultural rather than technical - are not overcome (Farre et al. 2010; Altman and Hasegawa 2012).

Social norms, culinary preferences and legal regulations are themselves culturally evolving systems that co-evolve with scientific knowledge and technological practices. Consequently, the acceptance and spread of agricultural practices and products may vary cross-culturally. For example, while large global commercial companies tend to invest mainly in major world staple crops (e.g., soybean, corn, canola, wheat, and rice), many other local plants remain "orphan crops". This is why the government of India, where eggplants are an important part of the diet, embarked on a mission to produce GM insect-tolerant Bt brinjal (eggplants). These were adopted rapidly, commercialized, but again some legislation problems and concerns were later raised (Kolady and Lesser 2012; Medakker and Vijayaraghavan 2007).

An appreciation of the social environment within which agricultural practices are situated, as follows from a CNC approach, has much in common with social science approaches that stress the embeddedness of new plant crops within socio-political contexts, not just performative qualities such as potential yield (Stone and Glover, 2017). Indeed, demand is growing recently for heirloom rice, traditional rice breeds that have lower yield than Green Revolution rice, but which are marketed as socially and environmentally responsible products embedded in local cultural traditions (Stone and Glover, 2017).

Case study 2: Plant stress tolerance/resistance

Major advances in molecular breeding have resulted in the genetic modification of crops to improve *biotic stress* resistance, including resistance to pests like insects, phytopathogenic fungi, viruses, nematodes, weeds and others (Ceasar and Ignacimuthu 2012; Gurr and Rushton 2005; Scholthof 2011; Suzuki et al. 2014; Vidavsky and Czosnek 1998), and *abiotic stress* tolerance, including tolerance to drought, salinity, extreme temperatures, heavy metal toxicity and others (Hirayama and Shinozaki 2010; Vinocur and Altman 2005; Zhu 2016). Two specific examples discussed here are herbicide and insect resistance.

Herbicide resistance was developed to combat weeds. With the intensification of agriculture, weeds became a serious economic threat to farming, resulting in increased agricultural production costs and yield loss of cultivated crops. This is especially the case in intensively grown and irrigated plants, that enhance weed growth in addition to the desired crop. This problem has been dealt with traditionally either by labour-intensive manual weeding, which is usually performed in less developed countries by women, by tillage, or by heavily spraying fields with large amounts of toxic herbicide chemicals that pollute the environment (Christensen 2009; Griepentrog and Dedousis 2009; Melander, Rasmusen and Barberi 2005). To avoid these costly solutions, weed management was simplified and manual work was reduced by genetically modifying crops to be herbicide resistant. This allows the use of considerably smaller amounts of broad-spectrum herbicides since they selectively kill only the weeds and not the crop (Bonny 2016; Gressel 2009). For example, herbicide-tolerant GM crops were created that express a soil bacterium gene that produces a glyphosate-tolerant or glyphosate-degrading form of an enzyme, resulting in glyphosate-tolerance (Castle et al. 2004) and resistance to commonly-used glyphosate herbicides. This cannot be achieved by traditional breeding. Currently, herbicide-resistance is the dominant trait deployed globally in soybean, maize, canola, cotton, sugar beet, alfalfa and other crops, and is being adopted increasingly rapidly by farmers comprising about 53% of the 180 million hectares of all GM crops in 2015/16 (ISAAA 2017).

Insect resistance provides crops with defences against herbivorous insects. Over the centuries farmers have selected plant varieties that are more resistant to insect pests. Like for herbicide resistance, traditional breeding for insect resistance was not very successful, and was followed from the 1940s by widespread spraying of fields with chemical insecticides. This had several drawbacks, including environmental pollution and damage to other non-pest organisms (Newton 1988; Weston et al. 2011). The biotechnological solution involved genetic modification of cultivated crops resulting in insect resistant plants where the specific pest is killed when it digests the plant. Insect tolerant GM cotton, potato, canola, corn, and other crops were developed through the introduction and expression of the soil bacterium *Bacillus thuringiensis* (Bt) *cry* genes in the GM plant, resulting in production of the endotoxin cry protein crystals that kill insect larvae upon digesting the leaves. This activity is selective and kills only specific target insect species pests (de Maagd, Bosch and Stiekema 1999). This technology has however several limitations, and improved methods have been developed recently, including genome-editing technology and “gene stacking”, i.e. the introduction and expression of multiple genes that create several toxic proteins (e.g. Gatehouse 2008; Lombardo et al. 2016).

The successive inventions and discoveries that led from traditional breeding and use of chemical pesticides to genetically-modified herbicide and insect tolerant plants constitutes another case of CCE. Each step is dependent on earlier innovations, and measures of improvement have increased, from crop yield and quality to reduced environmental harm. With our expanded definition of GCC to include non-human genes, the genetic modification of crops to incorporate bacterial genes to improve tolerance are also cases of GCC, given the culturally-driven changes in non-human genes.

Finally, traditional and molecular selection for stress tolerance constitutes an extensive example of CNC. Human efforts to genetically modify plants to improve their tolerance to biotic and abiotic stress has allowed the spread of cultivated plants into lands and regions where they could not have survived before. This involved the spread of organisms and their genes from one region of the world to another, either by straightforward domestication of new plant genes (e.g. the potato from Peru-Bolivia, and tomato from Chile, to Europe (Diamond 1977), see also Fig. 2 on gene transfer that accompanied the discovery of new lands), or by traditional breeding, or by gene transfer from any organism to the GM plants as mentioned above. All of these activities create new agricultural niches that then feed back to the agricultural process. The spread of agriculture is also associated with the spread of pests, which requires further changes to counter the pests, as described above. The use of both herbicide and insect tolerant crops reduces the amount of sprayed chemicals and thus can positively impact the environment, countering some of the negative consequences of the agriculturally-constructed niches (Pimentel 1995). It may also reduce the toxic effects of insecticides and other pesticides on human health (Levine and Doull 1992; Nicolopoulou-Stamati et al. 2016), as proposed for example as a cause of Parkinson's disease (van der Mark et al. 2012).

Like for golden rice, the impact on, and feedback with, the social environment is of great interest and importance. As noted above, women are the main work force in planting and weeding agricultural plots in many developing countries (Gressel 2009; Subramanian et al. 2010). In reducing the need for this time-consuming manual labour, GM herbicide tolerant crops can potentially relieve some of these economic hardships born by women and improve their socio-economic status by modifying the gender-biased division of labour. The spraying of herbicide tolerant GM corn and cotton in India, Africa and other regions has already saved many women from long working hours in the field and improved their economic situation and quality of life. Indeed, studies indicate that the education level of several women communities in certain regions in India, where herbicide tolerant crops were adopted, can increase significantly as they could devote more time to learning. Another recent study shows that biotechnology and the adoption of insect-resistant cotton in India generated more productive employment and greater earning power for women, and consequent improvement in quality of life (Agarwal 1984;

Subramanian 2010). For example, in India female laborers have benefited from the increased work hours—and thus increased income—associated with increased yields from *Bt* cotton because women pick the cotton (Subramanian and Qaim 2010). Similarly, a study in South Africa found that planting of *Bt* cotton was beneficial for women in the household; in this case, because women did not have to spray the crops, their energies could be diverted to other activities (Bennett et al., 2003). In Burkina Faso, fewer insecticide applications were needed for *Bt* cotton which meant women spent less time fetching water (Zambrano et al., 2013). Also, using herbicide-tolerant cotton in Colombia resulted in the hiring of fewer women for weeding, traditionally a female task (Zambrano et al., 2013). Moreover, there are some indications that, unlike with traditional crops, women in Colombia and the Philippines were found to participate equally with men in the decision-making and supervision of insect tolerant (*Bt*) cotton (Yorobe and Smale 2012).

Interestingly, these recent developments relating to gender roles may be reversing the historical effects of culturally evolving agricultural practices on gender-biased division-of-labor. Alesina et al. (2013) provide evidence that the introduction of the plough several centuries ago allowed men to control and monopolise food production, resulting in the loss of socio-economic power for women who had previously participated in food production.

Discussion

In summary, we have argued that new and complementary approaches within the evolutionary human sciences – cumulative cultural evolution (CCE), gene-culture coevolution (GCC) and cultural niche construction (CNC) (see Figure 1) – can provide theoretical frameworks for understanding the many impacts that agriculture has had on human societies and on the planet. Unlike prior papers that argue similarly (Heslop-Harrison and Scwarzacher 2012; O’Brien and Laland 2012), we have focused on recent biotechnology rather than the distant past, to both demonstrate that these frameworks are relevant for contemporary issues and events, and to make some novel points not apparent when focusing only on the past.

First, we argued that agriculture is an excellent case of CCE. It involves the sequential improvement over time of agricultural knowledge (both scientific and non-formal knowledge systems) and practices (from small-scale habits and routines to large-scale technology) via the repeated cycle of innovation and cultural transmission. Viewing changes in agricultural practices as an evolutionary process in itself, and recognizing the resultant coevolutionary dynamics and feedbacks, helps connect this cultural process with the biological/evolutionary/natural sciences, preventing a false and unproductive nature-culture dichotomy. Agriculture informally exhibits the classic exponential increase in knowledge and practices that is typical of CCE, with recent change seemingly orders of magnitude faster than past rates of change, and the large body of work exploring the drivers and inhibitors of CCE can be brought to bear on the study of agriculture.

Second, we argued that the standard notion of GCC, where human cultural practices shape human genes and vice versa, should be expanded to include culturally-driven changes in non-human genes. This includes, by definition, domestication, which entails the traditional breeding of domesticated species. More recently this has involved the direct genetic modification of other species with the introduction of GM crops. Our case studies, golden rice and herbicide/insect tolerant plants, are two of several other good examples of this (Shinozaki and Yamaguchi-Shinozaki 2007; Vinocur and Altman 2005).

Third, agriculture is a prime example of CNC, involving extensive modification of abiotic, biotic and social environments, and feedback from these environments back to agricultural knowledge and practices. Most interesting from our perspective are feedbacks with the social environment. Golden rice, and other GM crops, have received resistance from activist groups, political parties and regulators due to fears over food safety, genetic contamination and an aversion to ‘tampering with nature’. These concerns provoke increased regulation and safety testing within the agricultural industry to ensure that GM products are as safe as possible. While adequate levels of health regulation are of course needed, too-stringent regulation can prevent potentially beneficial innovations from spreading. The ideal outcome would be increased population health and reduced environmental impact as a result of GM crops such as golden rice, green super rice, and herbicide/insect resistant plants, as discussed here, as well as drought and salinity tolerant crops, post-harvest loss of food, use of novel fertility control in farm animals and more. Another positive social feedback is the impact on gender roles, with herbicide tolerant GM crops releasing women from tedious manual labour (weeding) and improving educational and economic outcomes. Figure 3 presents a schematic diagram of many of the processes that we have discussed, and their interactions.

[insert figure 3 here]

Theoretical frameworks are most useful if they highlight novel avenues of research, or provoke novel research questions. We suggest the following:

How does agricultural CCE operate?

As noted above, theoretical models and experiments suggest several complementary mechanisms upon which CCE depends, including high-fidelity social learning, selectively biased social learning targeted towards successful traits or individuals, recombination of disparate solutions, innovation that includes large risky leaps, and large (or partially connected) populations. Which of these is responsible for agricultural CCE could be addressed via archaeological and historical records, e.g. by quantifying the frequency and impact of different innovations (as done by Miu et al. 2018 for computer code) or the rate of recombination across different domains (as done by Youn et al. 2015 for patents). We might expect these mechanisms to change over time, or vary cross-culturally (Mesoudi et al. 2016). The cases of recent agricultural breeding technologies, as discussed above, afford the opportunity to study the drivers of CCE in real time, with richer datasets than those available to archaeologists and historians.

One interesting distinction already studied in the CCE literature is between intentional change by individuals (often called ‘guided variation’; Boyd and Richerson 1985) and unintentional change via the copying of successful traits or individuals (often called ‘direct’ or ‘indirect’ bias). This relates to debates in the archaeological literature over the extent to which domestication was intentional or unintentional (Abbo et al. 2014; Kluyver et al. 2017). Formal modelling of the kind used in the CCE literature may help to inform this debate, at the least highlighting how both processes can operate together, or vary in importance across different species, historical periods and societies, and should not be viewed as mutually exclusive. Molecular breeding seems to be under more precise control than traditional breeding, due to the fact that only specific genes are targeted rather than whole genomes of two traditionally-bred species, but still with unforeseen consequences especially in its social effects.

Finally, there are interesting questions regarding the ‘fitness’ criteria of agricultural CCE, i.e. the quantity that is being maximised (Mesoudi and Thornton 2018). An obvious criterion is crop yield (productivity) and nutritional content, but the discussion above has raised several additional criteria which may trade-off with these obvious criteria. Golden rice, for example, aims to maximise human health (by reducing Vitamin A deficiency) beyond simple calorific intake. Green super rice and herbicide tolerant GM crops aim to minimise environmental degradation. Heirloom rice explicitly trades off yield and productivity with embeddedness in the local producing community (Stone and Glover, 2017), albeit only applying to small-scale traditional farms and not to large-scale agricultural production. In this sense, the cultural fitness criteria that shape CCE are themselves evolving, amongst farmers, scientists and consumers.

CNC within social environments

We argued above that the most interesting niche construction dynamics involve feedback between agricultural practices and the social environment, e.g. social norms of consumers, regulatory bodies, and markets. Social norms also culturally evolve, partly according to the psychological biases of members of society that make some ideas or attitudes more likely to be recalled and transmitted than others, known as ‘content biases’ in the cultural evolution literature (Mesoudi 2011a). These may well affect moral norms concerning biotechnology (Mesoudi and Danielson 2008). For example, GM foods may violate psychological biases that provide us with ‘folk intuitions’ about the natural world (Atran 1998), including that species have discrete essences that are violated when genes are transferred across species. Similarly, people seem to have general psychological biases to attend to, recall and transmit disgust-eliciting stimuli (Eriksson and Coultas 2014), and moreover disgust-related taboos are more likely to occur against meat than plant products (Fessler and Navarrete 2003). This fits with evidence that there is more opposition to GM animals than GM plants (Schuppli and Weary 2010). Nevertheless, consumption of GM plants is still debated in many countries, mainly on the basis of health hazard concerns (Altman and Hasegawa 2012; Davison 2010; Echols 1998). Further experimental and observational work integrating the many psychological dimensions of norm transmission can be applied to norms surrounding biotechnology (Mesoudi and Danielson 2008).

There is evidence for cross-cultural differences in acceptance or rejection of GM foods. For example, consumers in the US seem much more accepting than EU consumers towards GM foods (Gaskell et al. 1999). Such differences demand explanation in terms of the divergent cultural histories of the different societies. Intriguingly, there is some evidence that agriculture and societal organisation have been co-evolving for millennia. Talhelm et al. (2014) show that historically rice-farming regions of China are more collectivistic than historically wheat-farming regions of China. They suggest that the intensive and demanding labor required by rice farming created closer social ties and social interdependence than the more independently-pursued wheat farming. For example, rice agriculture demands more water, and greater coordination of irrigation across plots of land; when rice is grown on steep hill slopes, as it often is, the farmer of one small slope must cooperate and coordinate with the farmers of plots above and below them to ensure adequate irrigation for all plots. Wheat farming, by contrast, requires less irrigation management and therefore less need to coordinate and cooperate across farms. In cases such as this, we see agriculture shaping social orientations, which may in turn shape the subsequent spread or acceptance of further agricultural practices.

Conclusion

Agriculture has transformed our species and our planet to such an extent that it is one of the primary reasons why some scholars advocate the renaming of the current epoch to the Anthropocene (Ellis 2015; Ellis et al. 2018; Lewis and Maslin 2015). The rapid rates of socio-cultural and scientific-technological change over the last century have only increased this impact, sometimes positive and sometimes negative. Here we have attempted to integrate several recent scientific-technological changes in agricultural knowledge and practices with an understanding of agriculture's impact on environments, including social environments, within novel theoretical frameworks of CCE, GCC and CNC.

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Conflict of Interest

The authors declare that they have of no conflict of interest.

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Figures

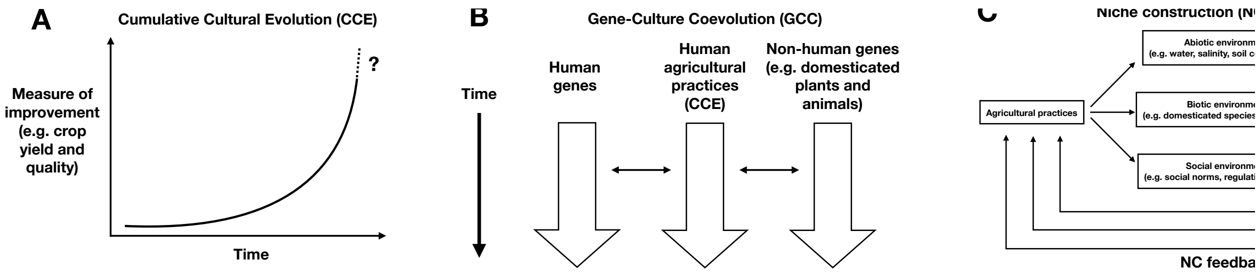

Figure 1: A schematic illustration of three approaches for understanding agriculture and plant breeding. (A) Cumulative cultural evolution (CCE) occurs as beneficial modifications are accumulated over time via repeated innovation and social learning, with an increase in some measure of improvement (e.g. crop yield and quality). (B) Gene-culture coevolution (GCC) typically describes the interaction between human genes and agricultural practices (an example of CCE), to which we add the additional interaction with non-human genes of domesticated animals and plants. (C) Cultural niche construction (NC) describes how agricultural practices may shape the abiotic, biotic and social environment, with those changes feeding back to shape agricultural practices.

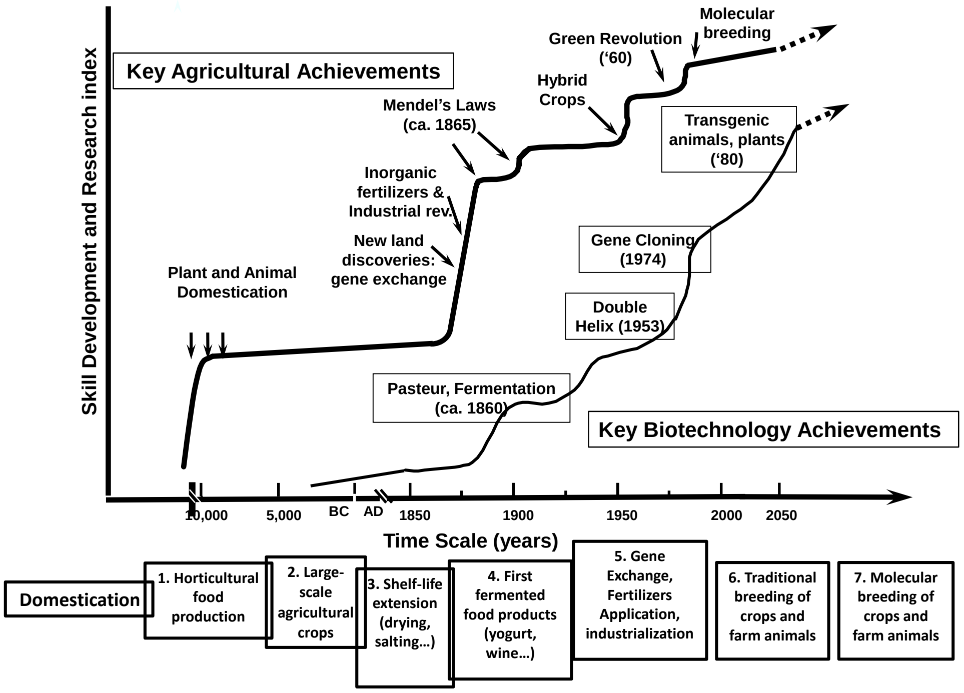

Figure 2: Key evolutionary events in agriculture and general biotechnology. Schematic illustration of cultural evolution of the major agricultural niches and sub-niches and accompanying technological and biotechnological innovations are depicted (**bold line**) as a relative skills and research index vs. the timeline (from the accepted start of agriculture, domestication, to present). The parallel evolution of general key biotechnological events is also depicted (standard line). Several major events in agricultural evolution are indicated with arrows pointing to the approximate time. The resulting major agricultural sub-niches are indicated in a series of encircled bold numbers above the timeline (1 to 7), at the approximately corresponding period: initial plant domestication resulted in small-scale horticultural food production (**1**); With further domestication, large-scale agricultural food production took place as a result of trial-and-error plant trait selection and agronomic improvements (**2**); As excess quantities of food became more available, people started to extend the shelf life of fresh food by preservation via drying, salting, smoking and other technologies, some of which were

practised already by hunters-gatherers (**3**) and by fermentation (Nummer 2002) (**4**); Three key events further enhanced food quantity and quality from the 13th century (**5**): (a) long distance travelling and discoveries of new countries resulted in imports and exports of new plants between countries, which allowed for new gene combinations, global gene exchange and domestication of new species, (b) introduction of agricultural machinery during the industrial revolution, foremost the steel plough, cotton gin, seed drills, and later tractors as well as (c) chemical synthesis of ammonia that resulted in massive use of nitrogen fertilizers and large increase in crop production (Erisman et al. 2008). Discovery of Mendel's laws of genetics and its rediscovery later, allowing revolutionary intentional science-based traditional breeding (Hallauer 2011) (**6**).This was followed by molecular breeding using genetic engineering, and more recently by genome editing (**7**).

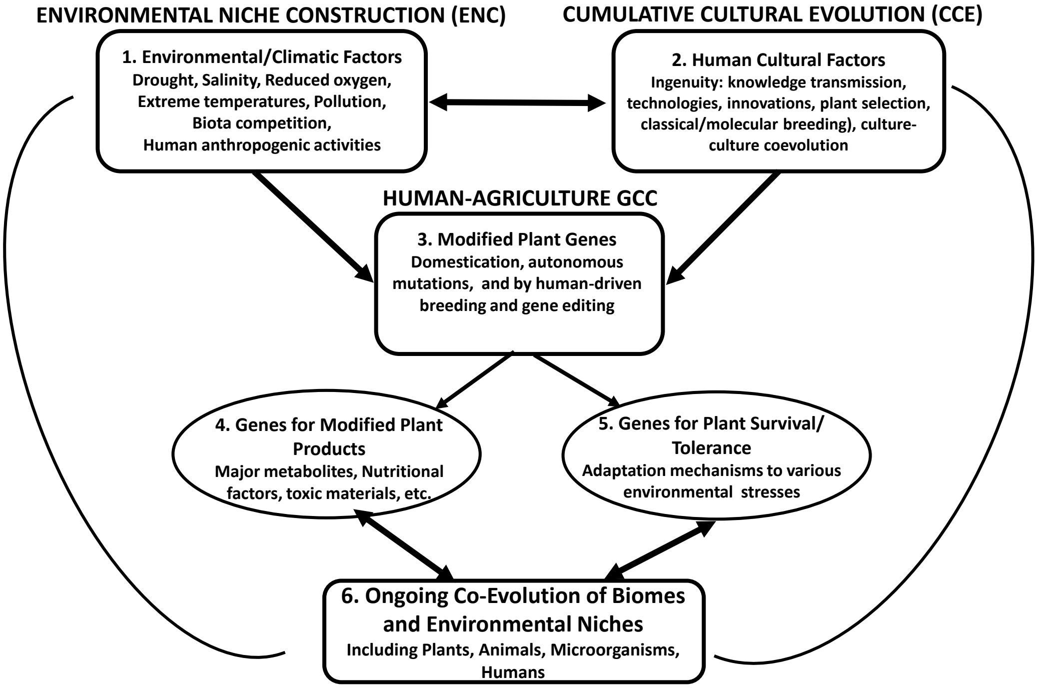

Figure 3: Major agriculture and culture-associated niche construction and plant gene-culture coevolution. The different interacting components of cumulative cultural evolution (CCE), plant-specific gene-culture coevolution (GCC), and environmental/agriculture-associated cultural niche construction (CNC) are schematically represented. Two major components are implicated: the physical environment, i.e., geography, the terrain, climate, and more (Box 1), human cultural factors, including ingenuity, technology and scientific discoveries (Box 2). Both may modify, shape, interact and coevolve with specific genes of domesticated plants (and farm animals) (Box 3). Once a certain selected gene combination has been fixed in a domesticated plant (or a farm animal) it can be again modified by traditional breeding techniques or by employment of novel molecular tools (MAS, GM, Genome editing) to produce novel gene combinations affecting mainly genes associated with modified plant products and metabolites (Box 4) and genes for improving plant survival/ tolerance to environmental stresses (Box 5). The novel plant products or traits can in turn result in the creation of new

environmental niches, affect the expression of human genes through consuming those products, resulting in ongoing coevolution of biomes (i.e., the entire complex body of living organisms including plants, animals, and microorganisms), CCE, GCC, and ENC (Box 6).